

SANDRO RUFFO* & AUGUSTO VIGNA TAGLIANTI**
 RICERCHE ZOOLOGICHE DELLA NAVE OCEANOGRAFICA
 "MINERVA" (C.N.R.) SULLE ISOLE CIRCUMSARDE. III.

DESCRIPTION OF A NEW CAVERNICOLOUS *INGOLFIELLA*
 SPECIES FROM SARDINIA, WITH REMARKS ON
 THE SYSTEMATICS OF THE GENUS

(CRUSTACEA, AMPHIPODA, INGOLFIELLIDAE) (1)

The faunistic and biogeographic researches on the small islands near Sardinia promoted by prof. Baccio Baccetti, carried out from 1985 up to the present and supported by the oceanographic ship "Minerva" of the National Research Council, also included a study of the fauna of subterranean waters, both interstitial and phreatic. The sampling effected by prof. Vezio Cottarelli in a freshwater pool in a cave of the island of Tavolara (northeastern Sardinia), led to the discovery of a new *Ingolfiella*, the first true cave-dwelling species of this genus. The first part of this article concerns the description of this new species.

An examination of the new species' relationships with, and its taxonomic position among, the different groups in which the 27 hitherto known species are distinguishable, led to a critical discussion of the main diagnostic characters used by various authors, to a study of more new material regarding some species, and lastly to proposing an arrangement of subgenera that does not coincide with the previously ones. This systematic revision of the genus *Ingolfiella* takes up the second part of the present paper.

***Ingolfiella cottarellii* n. sp.**

D i a g n o s i s - An *Ingolfiella* without ocular lobes, oostegites and ♀ pleopods, ♂ with only pleopod 1; similar to *I. catalanensis* and *I.*

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(1) Ricerche eseguite con contributi C.N.R. e M.P.I. (fondi 40%).

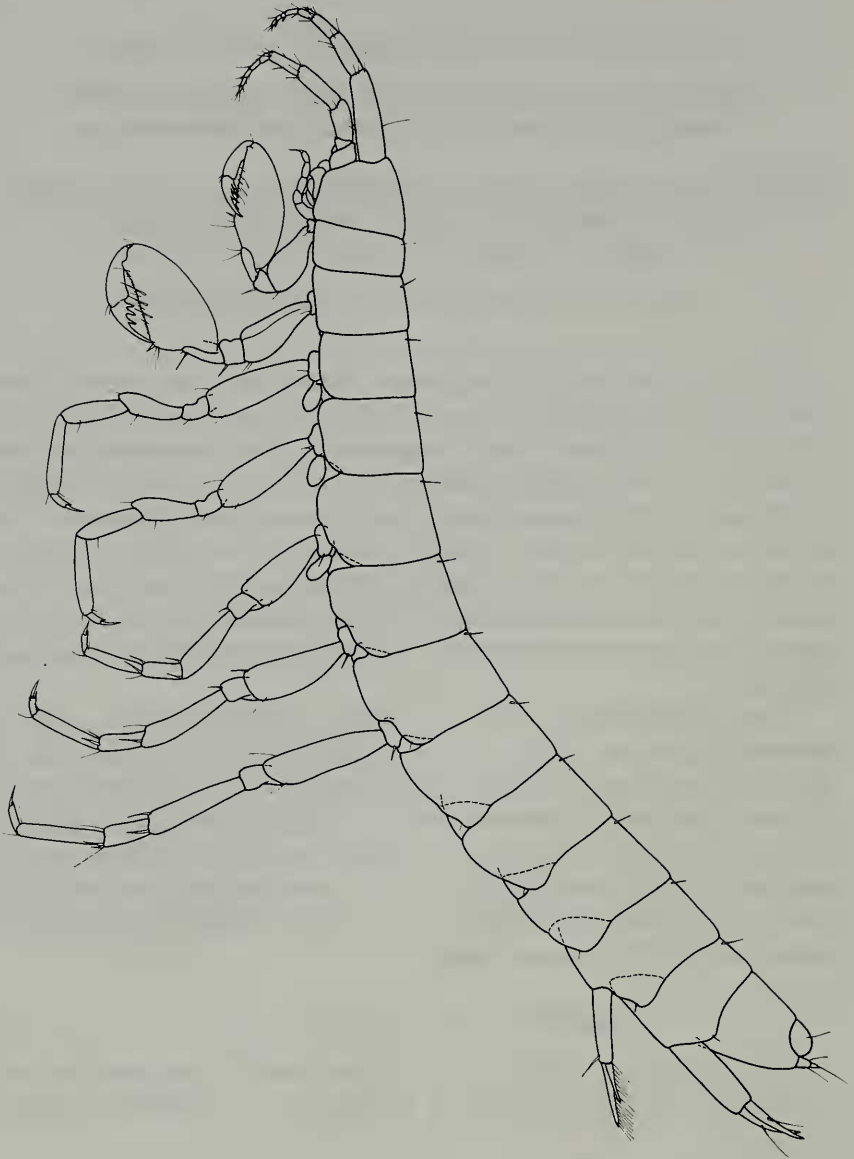


Fig. 1 - *Ingolfiella cottarellii* n. sp., Grotta del Papa (Tavolara Is., Sardinia), holotype ♀ 2.7 mm. Habitus.

thibaudi, strongly differing in carpus of gnathopod 2 with densely serrulate palmar margin, uropod 1 with longer exopodite and uropod 2 with 6-7 rows of spinules.

Material examined - Sardinia, Sassari Prov., Tavolara Island, Grotta del Papa, 29.VII.1986, V. Cottarelli leg., 4 ♂♂, 4 ♀♀, collected in a freshwater cave pool, in the dark zone, a few meters above sea level. The Grotta del Papa 87 SA/SS is a cave open at sea level near the Punta del Papa, on the eastern coast of the island of Tavolara, Olbia; Lat. 40° 54' 52", Long. 2° 42' 31"; altitude 0, length 140 m, development 175, difference in level +13 (Federazione Speleologica Sarda, 1984).

Accompanying fauna: Copepoda Harpacticoida and *Speocyclops* sp. (det. V. Cottarelli, 1986).

The holotype (♀, MVR Cr 233, slides 1924-1925) and the paratypes (1 ♂ on slides 1926-1927) have been deposited in the Museo Civico di Storia Naturale, Verona, except for the 1 ♂ 1 ♀ paratypes, which are in the Museo Civico di Storia Naturale, Genova.

Description - ♀ 2.5-2.7 mm. Body (fig. 1) not very elongate, laterally compressed. Head without ocular lobes, a little shorter than two first pereonites combined. Pereonites 1 the shortest, height twice the length, all body segments, particularly pereonites 6-7, pleonites 1-3 and urosomite 1, distinctly higher than long, each with 2 dorsal setules (except urosomite 3). Pereonites 4-7, pleonites 1-3 and urosomite 1 with lobiform plate on posteroventral corner, very short on pereonites 4-7, developed on pleonites 1-3 and urosomite 1, with 1 medial setule.

Antenna 1 (fig. 2a) peduncle articles 1:2:3 = 1:0.5:0.3, main flagellum 5-articulate, articles 2-4 each with an aesthetasc, article 5 with a distal element minutely sculptured; accessory flagellum 3-articulate, a little longer than article 1 of main flagellum, article 1 very short, article 3 with a minutely sculptured distal element. Antenna 2 (fig. 2b) peduncle articles 3:4:5 = 0.7:1:0.9, flagellum 5-articulate, article 5 with a distal element as in antenna 1.

Mouthparts basic. Mandibles (fig. 2c) with cutting edge tricuspidate, lacinia mobilis strong, bicuspidate, with 2 linguiform setulose processes; molar subconical, elongate, ending in bifurcate tip, with 1 subterminal setulose process. Labium (fig. 2d) with lobes widely separated, each with 2 short distal conical prominences (glandular?). Maxilla 1 (fig. 2e) outer lobe with 2 long plumose setae and 4

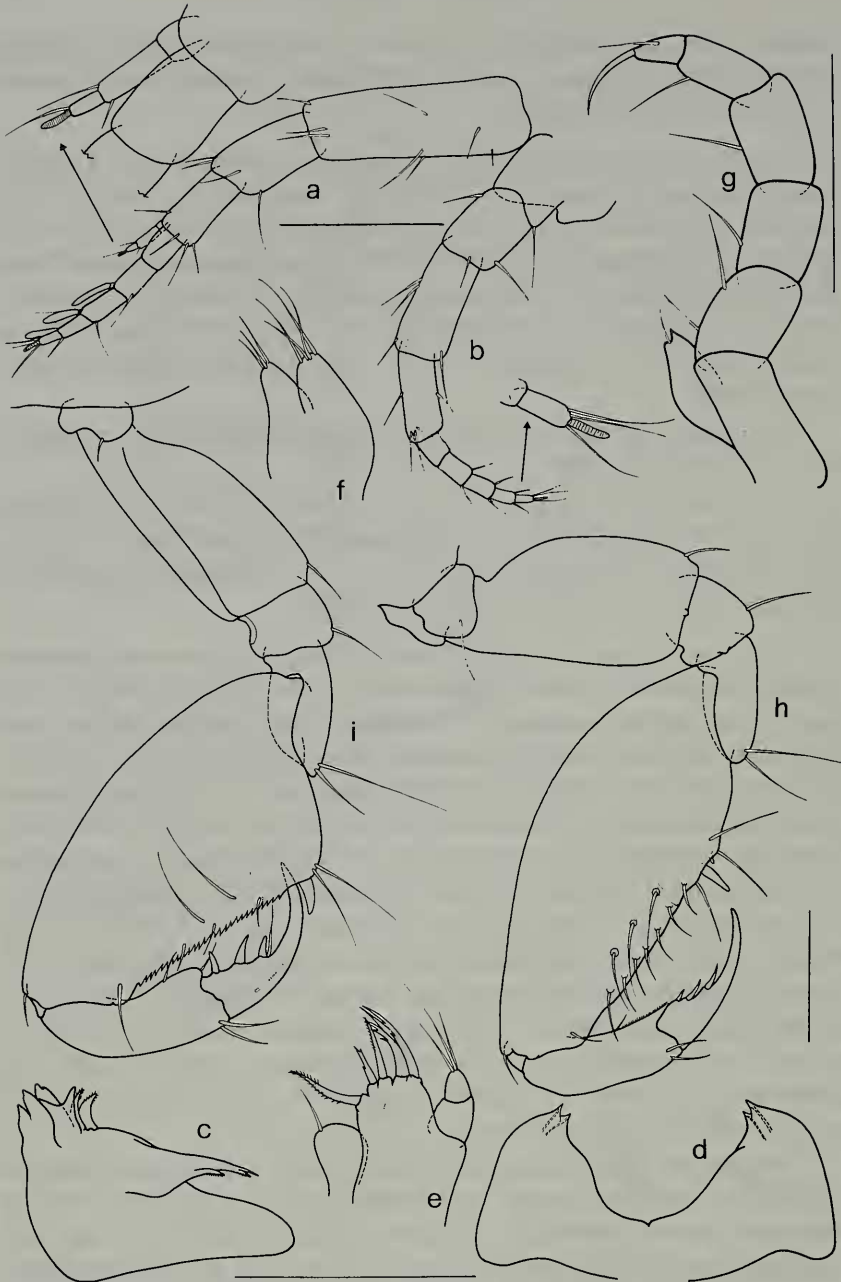


Fig. 2 - *Ingolfiella cottarellii* n. sp., Grotta del Papa (Tavolara Is., Sardinia), holotype ♀ 2.7 mm. a-b. Antennae 1-2. c. Right mandible. d. Labium. e-f. Maxillae 1-2. g. Maxilliped. h-i. Gnathopods 1-2. (Scales represent 0.1 mm).

denticulate spines, inner lobe rounded with 2 apical setae, palp 2-segmented with 3 distal setae. Maxilla 2 (fig. 2f) outer lobe with 4 apical setae, inner lobe with 3. Maxilliped (fig. 2g) endite small with distal notch and 1 seta, palp segments 1-4 of about same length, segment 5 conical, ending with very long unguiform spine.

Coxal plates very small (especially the first pair), with 1 seta on posterodistal rounded corner. Coxal gills on pereonites 3-5, suboval, slightly pedunculate (figs. 3a-b). Oostegites apparently lacking.

Gnathopods 1-2 dissimilar. Gnathopod 1 (fig. 2h) carpus ovoid, elongate; palmar margin defined by 1 strong spine and 2 setae, with 2 spines on inner side near palmar angle, a marginal row of 7 setae and a submarginal row of 3 longer setae on outer side; propodus minutely setulose along inner margin, dactylus with 3 spines on inner margin. Gnathopod 2 (fig. 2i) carpus subtriangular; palmar margin finely serrulate, with about 25 indentations, defined by 1 strong spine and 2 setae, with 1 spine on inner side and 2 long setae on outer side; propodus relatively elongate, dactylus with 3 strong articulate teeth.

Pereopods 3-4 (fig. 3a) similar, basic; propodus longer than carpus; dactylus elongate, basal part ending with sharp inner process, inner margin with some setules, claw as long as basal part, simple. Pereopods 5-7 (figs. 3b-d) increasing in length; merus elongate, especially in pereopod 7, with 1 strong spine on posterodistal corner; carpus short, in pereopods 5-6 with 1 strong spine on posterodistal corner, in pereopod 7 with 4 spines on posterodistal corner, one of these denticulate; propodus much longer than carpus, particularly in pereopod 7; dactyli almost identical to those of pereopods 3-4.

Pleopods totally absent.

Uropod 1 (fig. 4a) exopodite over half as long as endopodite, 2-segmented, endopodite with several long setae, trifid at tip. Uropod 2 (fig. 4b) peduncle with 6-7 rows of spinules, rami subequal, claw-like. Uropod 3 (fig. 3e) without peculiarities.

Telson (fig. 3e) fleshy, with 2 dorsal setules.

♂ 2.3-2.5 mm. Similar to ♀, but pleopod 1 present (figs. 4c-d) in form of elongate scale, with 2 apical setae. In the males examined a globular mass, probably a spermatophora (fig. 4c), was present at the base between pereopods 7.

Derivatio nominis - It is a pleasure to name this new species in honour of our colleague and friend prof. Vezio Cottarelli, who collected it during the "Minerva" expedition researches in the

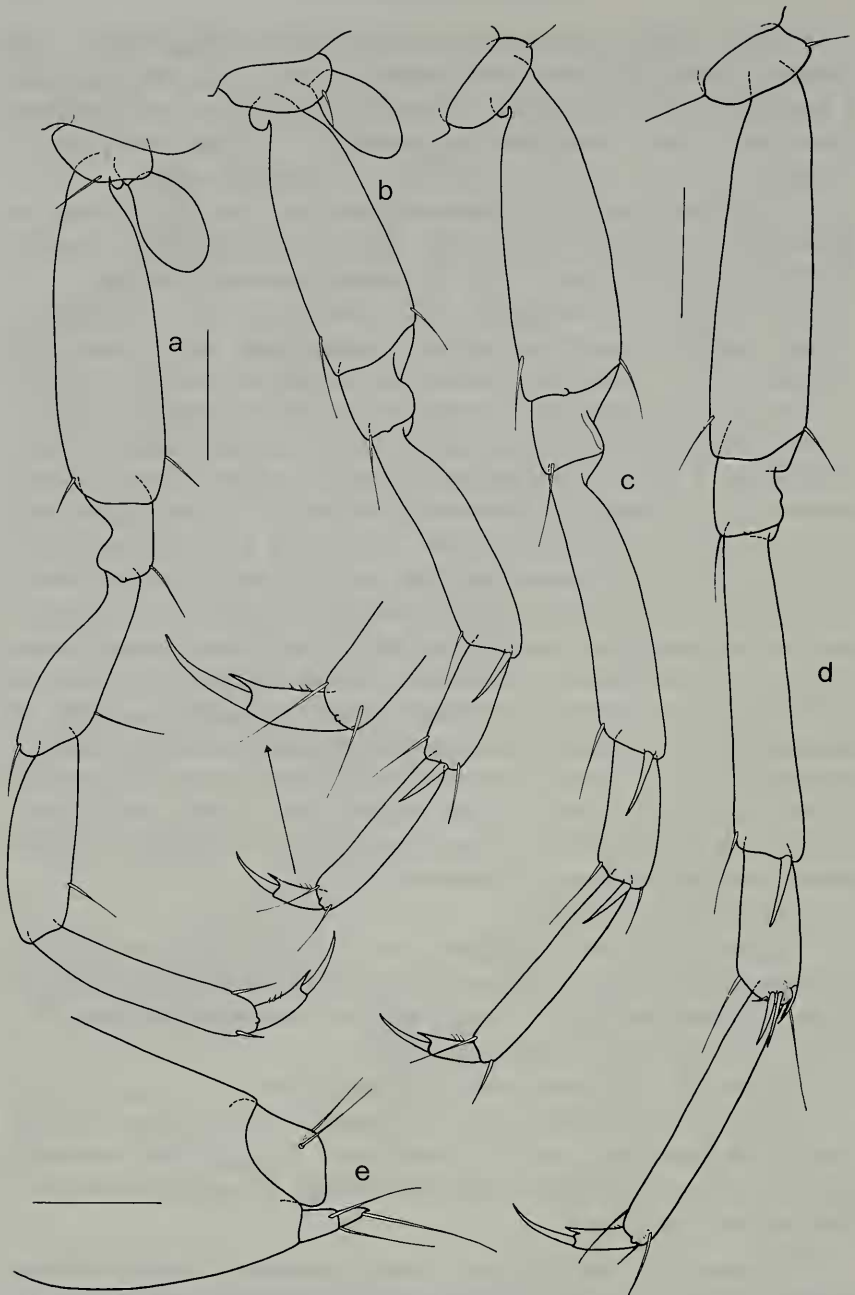


Fig. 3 - *Ingolfiella cottarellii* n. sp., Grotta del Papa (Tavolara Is., Sardinia), holotype ♀ 2.7 mm. a. Pereopod 3. b-d. Pereopods 5-7. e. Urosome with uropod 3 and telson. (Scales represent 0.1 mm).

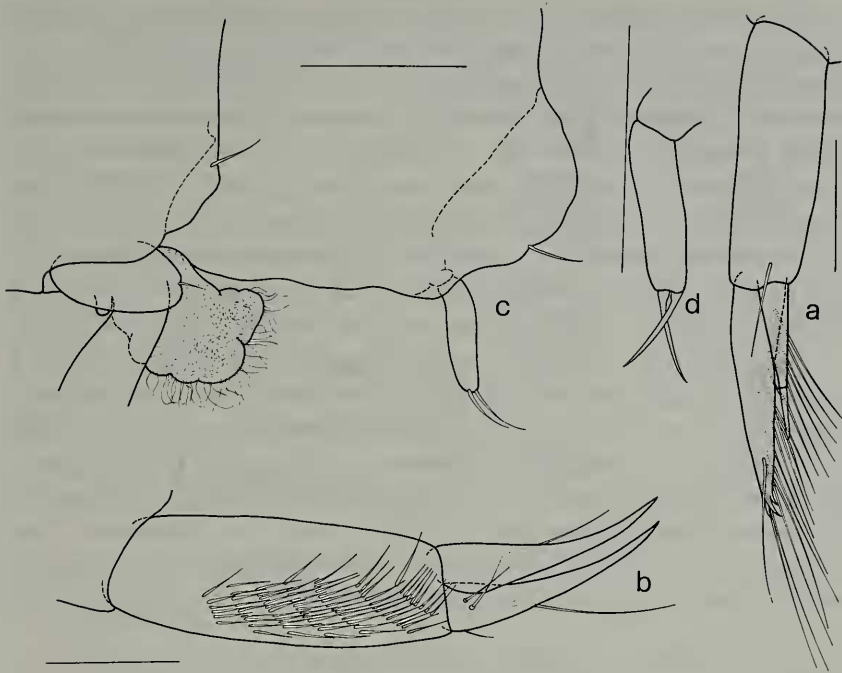


Fig. 4 - *Ingolfiella cottarellii* n. sp., Grotta del Papa (Tavolara Is., Sardinia), holotype ♀ 2.7 mm. a-b. Uropods 1-2. id., paratype ♂ 2.5 mm. c. Pereon segment 7 (with spermatophora) and pleon segment 1 (with pleopod 1). d. Pleopod 1. (Scales represent 0.1 mm).

small islands near Sardinia, for his valuable contribution to the knowledge of phreatic and interstitial fauna.

Remarks - *Ingolfiella cottarellii* n. sp., among all known *Ingolfiella* s. lato species, is particularly similar to *I. thibaudi* Coineau, 1968, from the interstitial fresh waters of the Gard and Ardèche valleys (Southern France). The main similarities consist above all in the following characters: ocular lobes lacking; ♀ pleopods 1-3 absent; only ♂ pleopod 1 present, elongate, scale-shaped; pereopods 3-7 dactyli identical, elongate, with long simple claw. *Ingolfiella cottarellii* is easily distinguishable from *I. thibaudi* by the shorter antenna 1 accessory flagellum, the more elongate gnathopods 2 carpus with palmar margin straight and finely serrulate, the longer pereopods, especially pereopod 7, uropod 1 with a longer exopodite, uropod 2 shorter, with peduncle bearing 6-7 rows of spinules.

Ingolfiella catalanensis Coineau, 1963 (see also COINEAU, 1968), from the interstitial fresh waters of Tech Valley (Pyrénées-Orientales, Southern France), is also similar to *I. cottarellii* in its lack of ocular lobes and ♀ pleopods, in the shape of ♂ pleopod 1 (the only one present) and in pereopods 3-7 having similar dactyli. *I. catalanensis* is quite different from *I. cottarellii*, even more than *I. thibaudi*, due to the following main characters: gnathopods 2 sexually dimorphic, with a differentiated element on ♂ carpus, «allongé terminé en biseau», in pereopods 3-7 dactyli, with an elongate claw finely bifid at the tip, and ♂ uropod 2 with a «hammer-like» spine at the basis of the peduncle.

In our opinion, therefore, *Ingolfiella catalanensis* Coineau, 1963, *I. thibaudi* Coineau, 1968 and *I. cottarellii* n. sp. form a well defined group of species, owing to the following combination of characters: 1) ocular lobes absent; 2) ♀ pleopods 1-3 absent; 3) ♂ pleopod 1 only present, digitiform; 4) pereopods 3-7 dactyli elongate and similar; 5) oostegites absent. All three species live in fresh water (two interstitial, one cavernicolous) and their distribution is biogeographically congruent, their localities occupying a marginal position in the "Tyrrhenian" area.

NOTES ON THE SYSTEMATICS OF THE GENUS *Ingolfiella* HANSEN, 1903

According to STOCK's systematics (1976, 1986), *Ingolfiella catalanensis* and *I. thibaudi* are to be referred to two different subgenera, namely *Gevgeliella* S. Karaman, 1959 and *Trianguliella* Stock, 1976, only in gnathopods 2 being sexually dimorphic in *catalanensis* and not dimorphic in *thibaudi* (as in *cottarellii*). Some doubt about the systematics of *Ingolfiella* as proposed by STOCK (1976) was expressed by one of us (RUFFO, 1985), and recently confirmed by DOJIRI & SIEG (1987).

In our opinion, it is now necessary to again examine the 27 known species of the genus *Ingolfiella* on the basis of a re-evaluation of the main diagnostic characters, thus tending to recognize «groups of species» that are more homogeneous from a morphological and biogeographical point of view.

For such an analysis we must examine separately those characters we can consider the most significant on a diagnostic level. In Table 1 the characters separately discussed below are listed, with an interpretation of their plesio- or apomorphic state.

Table 1 - List of the main diagnostic characters of the *Ingolfiella* species, with an indication of their plesio- or apomorphic state.

| Characters | plesiomorphous | apomorphic |
|---|----------------|-------------------|
| 1. Ocular lobes | developed | reduced or absent |
| 2. Pleopods 1-3 ♀ | present | absent |
| 3. Pleopods 2-3 ♂ | present | absent |
| 4. Pleopod 1 ♂ | triangular | digitiform |
| 5. Gnathopod 2 ♂, differentiated elements on carpus | absent | present |
| 6. Pereopods 3-4, claw | simple | dentate or bifid |
| 7. Pereopods 3-7, dactyli | similar | dissimilar |
| 8. Pereopods 5-7, dactyli | with claw | without claw |
| 9. Pereopods 3-7, basis of dactyli | not produced | produced |
| 10. Uropod 1♂, differentiated elements on peduncle | absent | present |
| 11. Uropod 2♂, basofacial spine on peduncle | absent | present |
| 12. Oostegites | present | absent |

1. Ocular lobes

Though the morphological and functional significance of the ocular lobes is still unknown, in our opinion their presence or absence (or reduction) is a character of great interest. They are always present in the sea water species (also in *Ingolfiella ruffoi* Siewing, 1958, originally described as lacking in ocular lobes; see fig. 5a) and are always absent in the species inhabiting true fresh water. One group of anchihaline cave- or brackish water-dwelling species (*Ingolfiella putealis*, *I. fontinalis*, *I. tabularis*, *I. margaritae*, *I. similis*) present ocular lobes variously reduced and perhaps absent.

2. Pleopods 1-3 ♀, and 3. Pleopods 2-3 ♂

Only the presence or absence of these pleopods is considered, and not their shape, which varies from subtrapezoidal or subtriangular (in most cases) to suboval, is more or less pointed and not easily and clearly definible.

4. Pleopod 1 ♂

In all species in which the male is known, even in those species lacking in female pleopods, the first pleopods of the male are always present. They are different in shape from the female pleopods, except for *I. ruffoi*. The sexual dimorphism of pleopod 1 is probably a

generalized character in the entire Ingolfiellidea suborder and is present also in *Trogloleleupia* Ruffo, 1974b, *Stygobarnardia* Ruffo, 1985 and *Metaingolfiella* Ruffo, 1969. Pleopod 1 ♂ in *Ingolfiella* is triangular-shaped, with 1-2 distal setae, or digitiform, with 2 apical setae: we consider the latter type to be in the apomorphic state, more differentiated from the generalized type.

5. Gnathopod 2 ♂, differentiated elements on carpus

In the apomorphic state the gnathopod 2 ♂ carpus has, immediately below the palmar margin, 1 variously modified and reversed seta. This differentiated element is "flanged" (*margaritae*, see STOCK, 1979), "pectinated" or "ciliated" (*putealis*, *fontinalis*, *tabularis*, see STOCK, 1976, 1977), «terminé en biseau» (*catalanensis*, see COINEAU, 1963), «en forme de sac» (*petkovskii*, see CVETKOV, 1964 and BOU, 1970) and a «processus en forme de lame hyaline porté par un pédoncule chitinisé» (*vandeli*, see BOU, 1970).

6. Pereopods 3-4, claw

The claw is always present on the pereopods 3-4 dactyli, simple (in the plesiomorphic state) or distally bifid or trifid, sometimes denticulate on the inner margin (in the apomorphic state).

7. Pereopods 3-7, dactyli

This character presents a similarity/dissimilarity in the shape of the dactylus between pereopods 3-4 and pereopods 5-7. In the apomorphic state, the dactyli of pereopods 5-7 are stouter than those in pereopods 3-4.

8. Pereopods 5-7, dactyli

In the primitive (plesiomorphic) state the dactyli of pereopods 5-7 have a separate claw, while the derivate (apomorphic) pereopods 5-7 dactyli lack a distinctly separate claw.

9. Pereopods 3-7, basis of dactyli

In the plesiomorphic state the dactyli of pereopods 3-7 have 1 spine at the basis of the claw that is lacking in the dactyli without a claw. In the apomorphic state the basal part of the dactylus is produced in a distal inner spur.

10. Uropod 1 ♂, differentiated elements on peduncle

The shape of uropod 1 is similar and generalized in all Ingolfiellidea, varying only in the length ratio of the exo-/endopodite.

Ingolfiella fuscina appears to be sexually dimorphic, with 1 pectinate reversed spine on the distal part of the peduncle in uropod 1 ♂. This species is closely related to the group of *I. xarifae*, *I. kapuri*, *I. quadridentata* and *I. longipes*, all four known only through the females: very probably these species could also be sexually dimorphic in uropod 1 (apomorphic state).

11. Uropod 2 ♂, basofacial spine on peduncle

In the plesiomorphous state the uropod 2 peduncle is similar in both sexes. In some species the uropod 2 ♂ peduncle has 1 basofacial spine that is usually distally hooked, but is hammer-like in *Ingolfiella catalanensis*. We consider the presence of the basofacial spine to be a character in the apomorphic state. As for uropod 2 in *I. thibaudi*, «un renflement de la base correspond à une protuberance du segment de l'urosome correspondant» (COINEAU, 1968): we cannot consider it sexually dimorphic nor indicate the state of this character.

12. Oostegites

In our opinion the presence of oostegites is a character in the plesiomorphous state. Frequently the authors do not give exact descriptions of this character. The presence or absence of oostegites is not indicated in the case of many species, even if the females are known; therefore one never knows whether oostegites are present or not, and even when their presence is confirmed, often their number and position are not given.

In the better known species, the oostegites are on pereonites 3-5 (*britannica*, *fuscina*) or 3-4 (*ischitana*, *quadridentata*). In a certain number of species, however, the oostegites seem to be totally lacking (species 19, 20, 23, 25-27, Table 2).

The oostegites have different shapes in the diverse species, but in this regard our knowledge is even more vague. Usually they are small, suboval, bearing 1 seta varying in length. In the case of *Ingolfiella quadridentata*, however, STOCK (1979) says they are «curved, truncate at tip, provided with 3 apical teeth, but without setae».

We feel it is inopportune to consider the character of the carpus of gnathopods 1 and 2 being similar or dissimilar in shape, which was already considered by STOCK (1976), because it is very difficult to make a clear-cut distinction.

Another character not considered at present is that of the uropod 2 rami: in some species they have been described or figured as «clearly 2-segmented» (STOCK, 1977), with a basal and more or less long, claw-ending, distal part; in other species the rami are “unimerous” and claw-like (STOCK, 1976). Many descriptions of this character are obscure and therefore rather unreliable.

In Table 2 we have considered the 12 characters discussed above for the 27 species of the genus *Ingolfiella* Hansen, 1903 known to date, and we have indicated the plesio- or apomorphic state of these characters.

This table shows that both sexes are known in only 13 species. As for the other 14 species, the males are unknown in 11 and the females in 3. Therefore it is not possible to consider those characters, in particular 5. and 11., related to sexual dimorphism. We can state that our knowledge is complete, or almost complete, only in the case of characters 1., 2., 6., 7., 8. and 9.

Table 2 demonstrates that, considering our present knowledge, it is possible to distinguish 7 groups of species, which can be only partially identified with those proposed by STOCK (1976, 1986) as subgenera of *Ingolfiella* Hansen, 1903.

Perhaps the above groups are genera but, in agreement with STOCK's cautious considerations (1976), we consider them for the present subgenera of *Ingolfiella*, especially in view of the fact that it is impossible now to correctly evaluate the characters related to sexual dimorphism.

Subg. **Ingolfiella** Hansen, 1903

Type species: *Ingolfiella abyssi* Hansen, 1903

Diagnosis - Ocular lobes developed. Pleopods present in females (males unknown). Pereopods 3-7 similar; dactyli elongate, with claw long, slender, apically sharp or very minutely bifid only in pereopods 3-4. Oostegites present.

Known species - *abyssi* Hansen, 1903; *britannica* Spooner, 1960 (assigned by STOCK (1976) to subg. *Hanseniella* S. Karaman, 1959); *atlantisi* Mills, 1967.

R e m a r k s - All species are marine and distributed in the North Atlantic; 2 are abyssal (*abyssi*, *atlantisi*), 1 is mesopsammic (*britannica*).

Ingolfiella ruffoi Siewing, 1958, a mesopsammic species from the coast of Peru, dubitatively assigned to *Hanseniella* by STOCK (1976), is also very close to *Ingolfiella* s. str. In the description (SIEWING, 1958) the species appears to be without ocular lobes and the maxillipeds seem to have no endites, but after examining some paratypes we ascertained

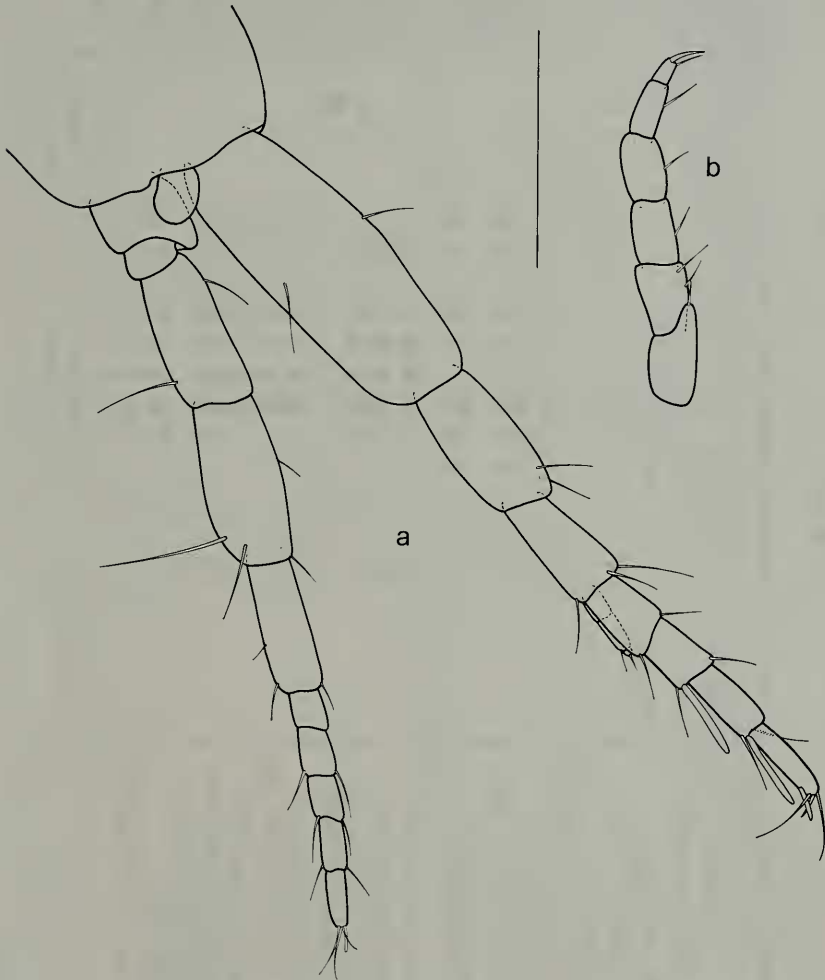


Fig. 5 - *Ingolfiella ruffoi* Siewing, 1958, 40 km north of Ilo (Southern Peru), locus typicus, paratype ♀ 1.4 mm. a. Head with antennae 1-2. b. Maxilliped. (Scale represents 0.1 mm).

Table 2 - List of the 27 species of the genus *Ingolfiella* Hansen, 1903 known to date, with indications of the state (hollow circle = plesiomorphous; solid circle = apomorphous) of the 12 main diagnostic characters and notes on their habitat (A = abyssal; B = mesopsammic; C = interstitial; D = cave; * = anchihaline) and distribution.

| Species | known sexes | | main diagnostic characters | | | | | | | | | | | | salt fresh water | | | | Distribution |
|---|-------------|---|----------------------------|---|---|---|---|---|---|---|---|----|----|----|------------------|---|---|---|------------------------------|
| | ♂ | ♀ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | A | B | C | D | |
| 1 <i>abyssi</i> Hansen, 1903 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | | | | NW Atlantic |
| 2 <i>ruffoi</i> Siewing, 1958 | + | + | ○ | ○ | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | + | | | S Peru |
| 3 <i>britannica</i> Spooner, 1960 | ? | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ○ | ○ | + | | | | NE Atlantic |
| 4 <i>atlantisi</i> Mills, 1967 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | | | | NW Atlantic |
| 5 <i>littoralis</i> Hansen, 1903 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | | | | Gulf of Siam (Indian Ocean) |
| 6 <i>berrisfordi</i> Ruffo, 1974a | + | — | ○ | ? | ○ | ○ | ● | ○ | ○ | ○ | ○ | ● | ? | ? | + | + | | | South Africa |
| 7 <i>ischantana</i> Schiecke, 1976 | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | Tyrrhenian Sea |
| 8 <i>xarifae</i> Ruffo, 1966 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | | | | Maldive Is. (Indian Ocean) |
| 9 <i>kapuri</i> Coineau & Rao, 1972 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | + | | | Andamane Is. (Indian Ocean) |
| 10 <i>grandispina</i> Stock, 1979 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | + | | | Curaçao (Lesser Antilles) |
| 11 <i>quadridentata</i> Stock, 1979 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | + | + | | | Curaçao (Lesser Antilles) |
| 12 <i>longipes</i> Stock, Sket & Iliffe, 1987 | — | + | ○ | ○ | ? | ? | ● | ○ | ○ | ○ | ? | ? | ? | ? | | | | * | Bermuda Is. |
| 13 <i>fuscina</i> Dojiri & Sieg, 1987 | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | South Carolina (NW Atlantic) |

follozus Table 2

| Species | known sexes | | main diagnostic characters | | | | | | | | | | | | salt water | | | | Distribution |
|--|-------------|---|----------------------------|---|---|---|---|---|---|---|---|----|----|----|------------|---|---|---|---|
| | ♂ | ♀ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | A | B | C | D | |
| 14 <i>putealis</i> Stock, 1976 | + | + | ● | ○ | ○ | ○ | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | * | | | | Bonaire Is. (Lesser Antilles) |
| 15 <i>fontinalis</i> Stock, 1977 | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | * | | | | Bonaire Is. (Lesser Antilles) |
| 16 <i>tabularis</i> Stock, 1977 | + | + | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | * | | | | Curaçao Is., Aruba Is. (Lesser Antilles) |
| 17 <i>margaritae</i> Stock, 1979 | + | — | ● | ? | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | * | | | | Isla de Margarita (Lesser Antilles) |
| 18 <i>similis</i> Rondé-Broekhuizen & Stock, 1987 | + | — | ● | ? | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | * | | | | Fuerteventura (Canary Islands) |
| 19 <i>pethkovskii</i> S. Karaman, 1957 | + | + | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | Yugoslavia, Bulgaria and Greece |
| 20 <i>vandeli</i> Bou, 1970 | + | + | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | Greece |
| 21 <i>acherontis</i> (S. Karaman, 1933) | — | + | ● | ○ | ? | ? | ○ | ○ | ○ | ○ | ○ | ? | ? | ? | + | | | | Yugoslavia |
| 22 <i>macedonica</i> (S. Karaman, 1959) | — | + | ● | ○ | ? | ? | ○ | ○ | ○ | ○ | ○ | ? | ? | ? | + | | | | Yugoslavia |
| 23 <i>manni</i> Noodt, 1961 | + | + | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | N Chile |
| 24 <i>uspallatae</i> Noodt, 1965 | — | + | ● | ○ | ? | ? | ○ | ○ | ○ | ○ | ○ | ? | ? | ? | + | | | | Argentine |
| 25 <i>catalanensis</i> Coineau, 1963 | + | + | ● | ● | ● | ● | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | South France |
| 26 <i>thibaudi</i> Coineau, 1968 | + | + | ● | ● | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | South France |
| 27 <i>cottarellii</i> Ruffo & Vigna Taglianti, 1989 | + | + | ● | ● | ● | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | + | | | | Sardinia |

that the species in fact presents very developed ocular lobes and a short endite on the maxilliped (figs. 5a-b). *I. ruffoi* differs from other *Ingolfiella* s. str. only in the dactyli of all pereopods being clearly bifid. In the case of *I. ruffoi* the males are also known: they present unmodified pleopods 1.

Subg. **Hanseniella** Stock, 1981 (= *Hanseniella* S. Karaman, 1959)

Type species: *Ingolfiella littoralis* Hansen, 1903

D i a g n o s i s - Ocular lobes developed. Pleopods present in males and females, pleopods 1 of males modified, subtriangular, with 2 apical setae. Dactyli of pereopods 3-4 unlike those of pereopods 5-7, with bifid or minutely denticulate claw; dactyli of pereopods 5-7 without claw. Uropods 2 not sexually dimorphic except in *I. berrisfordi* (only the male of which is known, however), in which the peduncle of uropod 2 presents 1 basofacial spine. Oostegites present in at least one species (*ischitana*).

K n o w n s p e c i e s - *littoralis* Hansen, 1903; *berrisfordi* Ruffo, 1974a (assigned by STOCK (1976) to subg. *Trianguliella* Stock, 1976); *ischitana* Schiecke, 1976.

R e m a r k s - All species of *Hanseniella* are marine mesopsammic, with Indo-Pacific-Mediterranean distribution.

Subg. **Tethydiella** novum

Type species: *Ingolfiella fuscina* Dojiri & Sieg, 1987

D i a g n o s i s - Ocular lobes developed. Pleopods present in females, probably also in males. In the only species in which the males are known (*fuscina*) the pleopods 1 are modified, subtriangular, with 1 apical seta. Gnathopods 2 not sexually dimorphic (*fuscina*). Pereopods 3-4 unlike pereopods 5-7; dactyli of pereopods 3-4 with claw elongate, apically bifid or trifold, sometimes minutely denticulate; dactyli of pereopods 5-7 with claw clearly stouter and stronger, apically bifid. In two species (*xarifae*, *quadridentata*), basal part of dactyli with sharp inner spur distally. Uropods 1 sexually dimorphic (*fuscina*). Oostegites present.

Known species - *xarifae* Ruffo, 1966; *kapuri* Coineau & Rao, 1972; *grandispina* Stock, 1979; *quadridentata* Stock, 1979; *longipes* Stock, Sket & Iliffe, 1987; *fuscina* Dojiri & Sieg, 1987.

According to STOCK (1976, 1979) *I. xarifae*, *I. kapuri* and *I. quadridentata* all belong to subg. *Hanseniella* S. Karaman, 1959 and *I. grandispina* to subg. *Trianguliella* Stock, 1976.

Remarks - The *Tethydiella* species are present in two discontinuous areas: the Indian Ocean (Andamane Is., Maldive Is.) and the tropical West Atlantic and Caribbean Sea (Bermuda Is., South Carolina, Lesser Antilles). All species are marine mesopsammic or cavernicolous in anchihaline caves (*longipes*).

Subg. **Antilleella** novum

Type species: *Ingolfiella tabularis* Stock, 1977

Diagnosis - Ocular lobes reduced, perhaps absent in some species. Pleopods always present; pleopods 1 modified in males, subtriangular, with 2 apical setae. Gnathopods 2 sexually dimorphic: carpus, in males, with large, modified, reversed seta. Pereopods 3-7 similar; dactyli with bifid claw, basal part with sharp inner spur distally. Uropods 2 sexually dimorphic with strong basofacial spine on peduncle of males. Oostegites probably always present.

Known species - *putealis* Stock, 1976; *fontinalis* Stock, 1977; *tabularis* Stock, 1977; *margaritae* Stock, 1979; *similis* Rondé-Broekhuizen & Stock, 1987.

These species were all assigned to subg. *Gevgeliella* S. Karaman, 1959 by STOCK (1976, 1977, 1979) and by RONDÉ-BROEKHUIZEN & STOCK (1987).

Remarks - The *Antilleella* species are known from wells with brackish water or from anchihaline caves (Lesser Antilles, Canary Is.) and probably represent the transition between the true marine species with clearly developed ocular lobes and freshwater species always without ocular lobes.

Subg. **Gevgeliella** S. Karaman, 1959Type species: *Ingolfiella petkovskii* S. Karaman, 1957

D i a g n o s i s - Ocular lobes absent. Pleopods always present; pleopods 1 modified in males, digitiform, with 2 apical setae. Gnathopods 2 sexually dimorphic: carpus, in males, with large, modified, reversed seta. Pereopods 3-7 similar, dactyli with bifid claw, basal part with sharp inner spur distally. Uropods 2 sexually dimorphic, with a strong basofacial spine on peduncle of males. Oostegites absent.

K n o w n s p e c i e s - *petkovskii* S. Karaman, 1957; *vandeli* Bou, 1970.

R e m a r k s - Interstitial and phreatic species, in fresh water, only known from Balkan Peninsula.

Subg. **Balcanella** S. Karaman, 1933Type species: *Balcanella acherontis* S. Karaman, 1933

D i a g n o s i s - Ocular lobes absent. Pleopods present in females. Dactyli of pereopods 3-7 similar, with claw long, slender, not bifid or denticulate. Oostegites apparently absent.

K n o w n s p e c i e s - *acherontis* (S. Karaman, 1933); *macedonica* S. Karaman, 1959; *manni* Noodt, 1961; *uspallatae* Noodt, 1965.

R e m a r k s - In all the species (except in *manni*) only the females are known and the species were therefore incompletely described. This may perhaps explain the extremely discontinuous, and therefore not very credible, distribution of this subgenus (Balkan Peninsula for the first two species, South America for the other two). It is probable that with more abundant material, including males, we can demonstrate a true heterogeneity among these four species, which were all collected in interstitial fresh water.

I. macedonica was assigned to subg. *Trianguliella* described by STOCK (1976) with a very heterogeneous complex of peculiarities (with or without ocular lobes, with or without pleopods, dactyli of pereopods 5-7 similar or dissimilar from those of pereopods 3-4). The type species of this subgenus, *I. manni* Noodt, 1961, from Chile, is certainly very similar to the *Balcanella* species, but a convincing comparison is not now possible, as the males of the other species are lacking. Therefore

for the moment we consider *I. manni* with reservations as part of the subg. *Balcanella*.

Subg. **Tyrrhenidiella** novum

Type species: *Ingolfiella cottarellii* Ruffo & Vigna Taglianti, 1989

Diagnosis - Ocular lobes absent. Pleopods 1-3 absent in females; pleopods 2-3 absent in males; pleopods 1, in males, elongate, digitiform, with 2 distal setae. Gnathopods sexually dimorphic or not; when dimorphic (*catalanensis*), carpus, in males, with large, modified, reversed seta. Pereopods 3-7 similar, dactyli elongate, with minutely bifid claw (*catalanensis*) or with simple claw; basal part only in *I. cottarellii* with sharp inner spur distally. Uropods 2 dimorphic or not; when dimorphic (*catalanensis*), males have basofacial hammer-like spine. Oostegites absent.

Known species - *catalanensis* Coineau, 1963 (assigned to *Gevgeliella* S. Karaman, 1959 by STOCK (1976, 1986); *thibaudi* Coineau, 1968 (assigned by STOCK (1976, 1986) to *Trianguliella* Stock, 1976); *cottarellii* Ruffo & Vigna Taglianti, 1989.

Remarks - The distribution of the *Tyrrhenidiella* species is paleotyrrhenic (Southern France: Depts. Pyrénées-Orientales, Gard, Ardèche; Sardinia). All are freshwater species, either interstitial or cavernicolous.

The above subgenera are distinguishable through the following key.

KEY TO SUBGENERA OF *Ingolfiella* HANSEN, 1903

- | | |
|--|-----------------------|
| 1. Pleopods present in males and females | 2 |
| - Pleopods absent in females; only pleopods 1 present in males. | |
| Ocular lobes absent | <i>Tyrrhenidiella</i> |
| 2. Dactyli of pereopods 5-7 without claw. Ocular lobes developed | <i>Hansenliella</i> |
| - Dactyli of pereopods 5-7 with claw | 3 |
| 3. Dactyli of pereopods 5-7 similar to those of pereopods 3-4 | 4 |
| - Dactyli of pereopods 5-7 dissimilar to those of pereopods 3-4. | |
| Ocular lobes developed | <i>Tethydiella</i> |

4. Basal part of dactyli of pereopods with sharp inner spur 5
 – Basal part of dactyli of pereopods without sharp inner spur 6
5. Pleopods 1 in males triangular with 1-2 apical setae. Ocular lobes reduced or absent *Antilleella*
 – Pleopods 1 in males digitiform with 2 apical setae. Ocular lobes absent *Gevgeliella*
6. Ocular lobes developed *Ingolfiella*
 – Ocular lobes absent *Balcanella*

GENERAL REMARKS

The incompleteness of the data concerning the 12 main diagnostic characters under consideration and probably the insufficient knowledge of other characters not considered here, do not allow for a correct cladistic analysis of the genus *Ingolfiella* on a species level. In fact, given the large number of unsolved questions in Table 2, it is not possible to analyze the characters of the 27 species in this genus. Therefore we have attempted to effect this analysis only for the 7 subgenera, which have been presented and described above. In each of these subgenera the state of the 12 main diagnostic characters is known for at least one species. We therefore think it is possible to attribute to the entire group of species (at the subgenus level) the known state of each character of the species in which this character is known. This can be seen in Table 3.

Table 3 - State (hollow circle = plesiomorphous; solid circle = apomorphous) of the 12 main diagnostic characters of *Ingolfiella* subgenera (names abbreviated).

| Character | ING | HAN | TET | ANT | GEV | BAL | TYR |
|-----------|-----|-----|-----|-----|-----|-----|-----|
| 1. | ○ | ○ | ○ | ● | ● | ● | ● |
| 2. | ○ | ○ | ○ | ○ | ○ | ○ | ● |
| 3. | ○ | ○ | ○ | ○ | ○ | ○ | ● |
| 4. | ○ | ○ | ○ | ○ | ● | ● | ● |
| 5. | ○ | ○ | ○ | ● | ● | ○ | ● |
| 6. | ● | ● | ● | ● | ● | ○ | ● |
| 7. | ○ | ● | ● | ○ | ○ | ○ | ○ |
| 8. | ○ | ● | ○ | ○ | ○ | ○ | ○ |
| 9. | ○ | ○ | ● | ● | ● | ○ | ● |
| 10. | ○ | ○ | ● | ○ | ○ | ○ | ○ |
| 11. | ○ | ● | ○ | ● | ● | ○ | ● |
| 12. | ○ | ○ | ○ | ○ | ● | ● | ● |

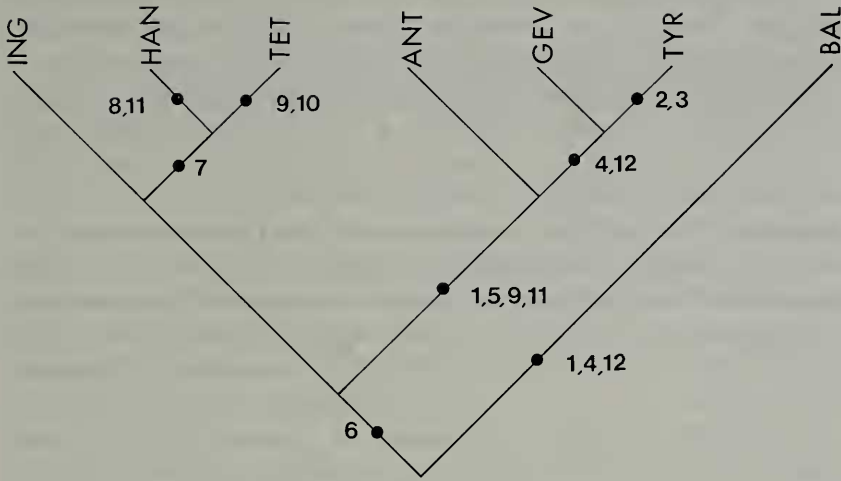


Fig. 6 - Cladogram obtained with the Camin-Sokal parsimony method by the MIX program and appraised by CONSENSE program of the Phylip 3.0 package of phylogenetic inference.

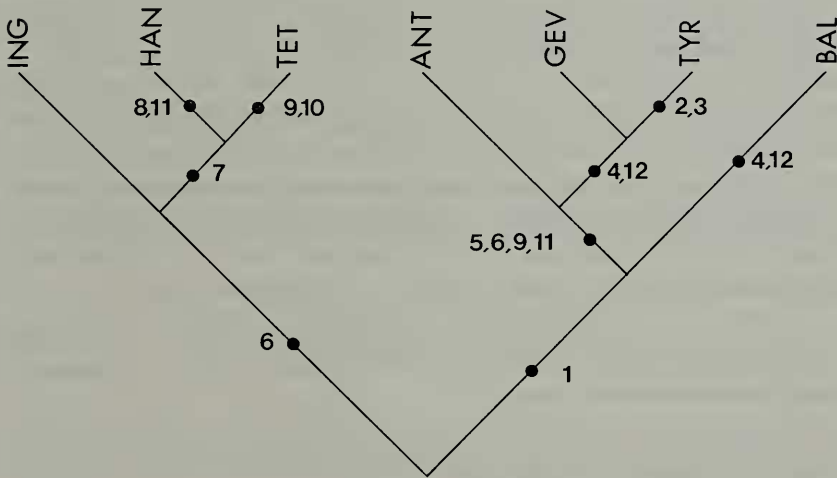


Fig. 7 - Cladogram obtained with the Camin-Sokal parsimony method by the MIX program of the Phylip 3.0 package of phylogenetic inference, with parallelisms in character 6. rather than in character 1.

The 12 diagnostic characters in Table 3 have been analyzed (analysis effected by dr. Maurizio Biondi, 1988) by using the MIX program included in the Phylip 3.0 package of phylogenetic inference (FELSENSTEIN, 1985), following the principles of cladistics with the Camin-Sokal and Wagner parsimony methods. The trees singled out by the MIX program were appraised by the CONSENSE program of the above-mentioned package in order to find the statistically most probable tree. The tree in fig. 6, obtained with the Camin-Sokal method, seems to correspond most to our phylogenetic hypotheses; this method contemplates $0 \rightarrow 1$ and not $1 \rightarrow 0$ state changes, with 17 steps and only 5 parallelisms. Of the 8 trees obtained with the Camin-Sokal method, however, there is also the one seen in fig. 7, also with 17 steps and 5 parallelisms, that differs from the preceding one only in the presence of parallelisms in character 6. instead of character 1. The greater statistical probability of the tree in fig. 6 is based on the assumption that all the characters are of equal importance. But in critically evaluating the individual characters, it seems more correct to admit of the possibility of parallelisms in character 6. (pereopods 3-4 claw simple or dentate/bifid) rather than in character 1. (ocular lobes developed or reduced/absent), and thus we prefer the tree in fig. 7.

Some considerations can be made from this latter cladogram:

1. The genus *Ingolfiella* is divided into two groups of subgenera characterized by the presence, and respectively by the absence or reduction, of the ocular lobes. The first group, with species that probably have oostegites, is connected to sea water (*Ingolfiella*, *Hanseniella*, *Tethydiella*); the second group, whose species (except *Antilleella*) lack oostegites, is on the other hand connected to continental fresh or anchihaline water (*Antilleella*, *Gevgeliella*, *Tyrrhenidiella*, *Balcanella*). These two groups thus seem to be well defined from an ecological point of view, as has already been pointed out by RUFFO (1970).

2. The group of species with ocular lobes, particularly *Ingolfiella*, seems to be the most primitive, with the greatest number of characters in the plesiomorphous state.

3. The group of species with reduced/absent ocular lobes includes a relatively primitive subgenus (*Balcanella*), another one (*Antilleella*) in an intermediate position (and perhaps the presence in anchihaline or brackish water is not casual), and two decidedly more evolved subgenera (*Gevgeliella* and *Tyrrhenidiella*) with a large number of cha-

racters in the apomorphic state and from interstitial, phreatic and fresh water cave environments.

4. All the subgenera have a significant geographic distribution except for *Balcanella*, whose composition, as we have said above, gives rise to many doubts.

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RIASSUNTO

UNA NUOVA *Ingolfiella* CAVERNICOLA DELLA SARDEGNA E NOTE SULLA SISTEMATICA DEL GENERE (CRUSTACEA, AMPHIPODA, INGOLFIELLIDAE)

Viene descritta *Ingolfiella cottarellii* n. sp., rinvenuta in una pozza d'acqua dolce all'interno di una grotta dell'isola di Tavolara, Sardegna nordoccidentale, prov. Sassari (Grotta del Papa 87 SA/SS). La specie, caratterizzata dall'assenza di lobi oculari, di oostegiti e di pleopodi (nelle femmine) e con il solo I paio di pleopodi (nei maschi), è simile ad *I. catalanensis* ed a *I. thibaudi*, con le quali costituisce un gruppo ben differenziato nell'ambito del genere *Ingolfiella*.

Il riesame della sistematica del genere *Ingolfiella* proposta da STOCK (1976, 1986) ha condotto a considerare 12 caratteri (Tabella 1) ed a discuterne lo stato di plesio-apomorfia. I risultati sono riassunti nella Tabella 2, che evidenzia l'esistenza di 7 gruppi più omogenei di specie, solo in parte coincidenti con i sottogeneri fino ad ora proposti.

A tali gruppi di specie viene attribuito il rango di sottogeneri: *Ingolfiella* Hansen, 1903, con 3 specie + 1 assegnata dubitativamente; *Hanseniella* Stock, 1981, con 3 specie; *Tethydiella* subg. nov., con 6 specie; *Antilleella* subg. nov., con 5 specie; *Gevgeliella* S. Karaman, 1959, con 2 specie; *Balcanella* S. Karaman, 1933, con 3 specie + 1 assegnata dubitativamente; *Tyrrhenidiella* subg. nov., con 3 specie.

L'analisi cladistica dei caratteri dei 7 sottogeneri così definiti (Tabella 3) ha portato a costruire un cladogramma, da cui si evidenziano i più probabili rapporti filogenetici tra i sottogeneri: ne risultano due gruppi di sottogeneri caratterizzati dalla presenza e rispettivamente dall'assenza o riduzione dei lobi oculari. Il primo gruppo è legato alle acque salate marine, il secondo a quelle continentali dolci o salmastre e anchihaline.

SUMMARY

Ingolfiella cottarellii new species from a freshwater pool in a cave on the island of Tavolara (NE Sardinia), the first true cave dwelling species of this genus, is described. This species, without ocular lobes, oostegites and ♀ pleopods, ♂ with only pleopod 1, is very similar to *I. catalanensis* and *I. thibaudi*, strongly differing only in the shape of gnathopods 2 carpus and uropods 1 and 2. A well characterized group of species (*Tyrrhenidiella* n. subg.) is therefore recognized.

An examination of the new species' relationships with, and its taxonomic position among, the different groups in which the 27 known species are distinguishable, led to a critical discussion of the main diagnostic characters, to a study of more new material regarding some species (a redescription of some characters of *I. ruffoi* is also given), and to proposing a new arrangement of subgenera. The genus *Ingolfiella* Hansen, 1903 is therefore divided into: *Ingolfiella* Hansen, 1903 (3 species, plus one assigned dubitatively); *Hanseniella* Stock, 1981 (3 species); *Tethydiella* n. subg. (6 species); *Antilleella* n. subg. (5 species); *Gevgeliella* S. Karaman, 1959 (2 species); *Balcanella* S. Karaman, 1933 (3 species, plus one assigned dubitatively); *Tyrrhenidiella* n. subg. (3 species). All these subgenera are described and discussed, and a key is given.

A cladistic analysis of the 12 main characters for the 7 subgenera is attempted. The resulting cladograms are also discussed, leading to the conclusion to divide the genus *Ingolfiella* into two groups of subgenera: the first, with ocular lobes developed and connected to sea water, is more primitive; the second, with ocular lobes reduced or absent and connected to continental fresh or anchihaline water, includes intermediate or decidedly more evolved subgenera.